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Changes in size, status, and distribution of badger *Meles meles* L. setts during a 20-year period

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Abstract

The size, status (whether "main setts" or "outliers"), and distribution of badger setts were compared using data from two separate surveys, begun in 1970 and 1990 respectively, of a 22 km^2 area in the south of England. During the period separating the two surveys, 24 main setts and 11 outliers persisted without a change of status; 1 main sett became an outlier and 14 outliers became main setts; 32 main setts and 131 outliers appeared de novo; and 5 main setts and 10 outliers disappeared. Main setts that persisted grew in size at an average rate of about 0.5 entrances per year. Changes in the status of a sett were not related to its initial size or habitat characteristics, but habitat changes or human interference were implicated in all cases in which main setts disappeared. Total number of main setts increased from 30 to 70, average territory size decreased from 0.7 km^2 to 0.3 km^2 and the number of outliers per territory increased from 1.2 to 2.0. The results suggest that when a badger population expands, new main setts are sometimes formed from existing outliers but are more often constructed de novo. Sometimes a main sett commanding a large territory is replaced by several new main setts and the territory is subdivided; on other occasions the original main sett persists and its territory is compressed as new territories are established in the vicinity.

Key words: *Meles meles*, mammal, burrow, distribution, territory

Introduction

Like many mammals (see review by Reichman and Smith 1990), badgers *Meles meles* L. are semi-fossorial: they are active on the surface at night, but sleep during the day in communal burrows known as "setts" (Neal 1977). The permanent place of residence of each social group is typically a single "main sett", distinguished by the fact that it is the largest burrow in the territory, is continuously occupied, and is used for breeding and overwintering (Neal 1977; Kruuk 1978; Roper and Christian 1992). Main setts are a traditional resource, handed on from generation to generation within a social group, as a consequence of which they can be continuously occupied for decades or even centuries (Neal and Roper 1991). Since successive occupants of a sett continue to enlarge it, ancient main setts can become extremely extensive: for example, Roper et al. (1991) describe a main sett of unknown age that possessed an estimated 50 nest chambers, 178 entrances and 879 m of underground tunnels (see Roper 1992 for other examples).

In addition to providing themselves with a main sett, badgers also often possess a number of smaller setts or "outliers", which are scattered around the territory and are only intermittently occupied (Kruuk 1978, 1989). These setts vary considerably in size: they can have from one to a dozen or more entrances and differ to a corresponding degree in the length of the underground tunnel network and the number of nest chambers

that they contain (e. g., Roper 1992; Roper et al. 1992). Thus badgers are remarkable amongst burrowing mammals for both the total amount and the diversity of underground space with which they provide themselves.

Although it is generally agreed that the size of a main sett is an indication more of its age than of the number of animals inhabiting it (Kruuk 1978; Neal 1986; Neal and Roper 1991), there are no data available on the rate at which main setts increase in size over time. In addition, although it is relatively clear how the possession of an adequate main sett contributes to survival and reproduction in the animals occupying it (Neal and Roper 1991; Roper 1992), it is less obvious why a social group of badgers that already possesses a main sett should also require one or more outliers within its territory. One possibility is that main setts and outliers constitute substitutable reservoirs of underground space, such that the possession of outliers compensates for a main sett that is relatively small in size and cannot be extended any further (Ostler 1994). In this case, there should be an inverse correlation between the size of a main sett and the number of outliers that the corresponding territory contains. Another possibility is that as a badger population expands and new social groups form, outliers may become converted into main setts (Neal and Cheeseman 1996). In this case, we would expect to see setts changing their status during the course of time.

Our study aimed to test these predictions by examining changes in the size, status, and distribution of individually identifiable main and outlier setts over time. We compared data from two detailed sett surveys of the same 22 km^2 area, undertaken in the early 1970's and the early 1990's respectively. As well as determining the size and characteristics of all setts within the area, we estimated territory boundaries using the method of Dirichlet tesselations (Upton and Fingleton 1985; Doncaster and Woodroffe 1993). This enabled us to examine the distribution of outliers across individual territories and also to visualise changes in territory size and shape that occurred as a consequence of new main setts becoming established.

Material and methods

Survey methods

The survey area covered 22.4 km^2 of contiguous South Downs farmland (see Roper et al. 1995 for further details). The site was surrounded on all sides by busy roads but, other than farm tracks for occasional vehicles, it was devoid of any attenuating or dividing topographical features such as roads, rivers or walls. Stopping of setts by fox hunters (Lindsay and Macdonald 1985) was not practised in the area and in general, human interference was negligible except for agricultural activities.

The first of the two surveys was undertaken by E. D. Clements in May, June, August, and October of 1971, 1972, and 1974 (see Clements 1974; Clements et al. 1988 for details). Locations of setts were marked onto 1 : 25 000 scale maps and information about type of sett, number of entrances, type of surrounding habitat (e. g., unimproved grassland, woodland etc.) and presence or absence of cover was noted down in the field and subsequently transferred to index cards. Entrances were classified as "used" if they were free of debris such as sticks or leaves. The second survey was carried out by J. R. O. during November–February 1991/1992 and 1992/1993 and followed, as far as possible, the procedures described by Clements (1974).

When analysing the two sets of survey data, care was taken to use the same criteria for classifying setts and habitat types. Setts were classified as "main setts" or "outliers" according to Mammal Society guidelines (Harris et al. 1989; Cresswell et al. 1990). We did not subdivide outliers into the separate categories of "subsidiary setts" and "annexes" (Kruuk 1978; Thornton 1988), since the distinctions between these are arbitrary and to a large extent subjective (Neal and Roper 1991). Thus, we use the term "outlier" to refer to any sett that was not a main sett.

Comparing results from the two surveys for purposes of analysis, it was possible to identify four possible outcomes as regards any one sett: a) a sett could persist from 1970 to 1990 without a change of status, i. e., a main sett could remain as a main sett, an outlier as an outlier; b) a sett could persist from

1970 to 1990 but change its status, from main sett to outlier, or vice versa; c) a sett could be new, i. e., have arisen de novo since the 1970 survey; d) a sett could have disappeared, i. e., be present in the 1970 survey but not in the 1990 survey. Setts were classified as having disappeared if no trace of them could be found despite thorough searching of the relevant area, or if nothing remained of the sett except overgrown and flattened spoil heaps, or entrances that were overgrown and completely blocked with soil, indicating that they had been abandoned for some years.

For purposes of analysis, we used total number of entrances as a measure of sett size. Data from excavated setts show that the number of entrances correlates well with other indices of sett size such as the area occupied by the underground tunnel system, the total length of tunnels, and the number of nest chambers (ROPER 1992).

Use of Dirichlet tesselations to estimate territory boundaries

Dirichlet tesselations provide a method of spatial analysis by which a pattern of points (in this case, locations of main setts) can be described in terms of the positions of each individual point relative to the positions of its immediate neighbours (UPTON and FINGLETON 1985). The method assumes that territory boundaries occur half way between adjacent pairs of setts and are oriented orthogonally to a line joining the two setts. When used to generate hypothetical congruent polygonal territory boundaries, the tesselations correspond reasonably well with real territory boundaries determined by bait-marking or radiotracking (DONCASTER and WOODROFFE 1993; OSTLER 1994).

Results

Inter-observer reliability

Since an element of subjectivity inevitably entered when sett entrances were classified as used or unused, it was necessary to compare the two surveys for inter-observer reliability. To do this we plotted the number of used entrances against the total number of entrances for 24 main setts for which data were available in both surveys. We predicted that if the same criteria were being used by both observers to classify entrances as "used", the ratio of used to total entrances should be the same for both datasets. This prediction was supported: the regression lines yielded by data from the two surveys were not significantly different in either slope ($T = 0.756$, $p = 0.453$) or intercept ($T = -1.352$, $p = 0.183$).

Setts persisting from 1970 to 1990 without a change of status

Twenty-four main setts and 11 outliers maintained their status over the 20-year period (Tab. 1). The main setts increased in size between 1970 and 1990 (Wilcoxon test, $Z = 3.17$, $N = 24$, $p < 0.01$), growing on average by about one new entrance every two years (see Tab. 2). There was no significant difference in the number of used entrances per main sett in 1970, by comparison with the number in 1990 (Wilcoxon test, $Z = -0.32$, $N = 25$, $p = 0.74$). However, there was a significant correlation between total number of entrances and number of used entrances in both surveys (Spearman test; 1970 data: $r_S = 0.39$, $N = 24$, $p = 0.056$; 1990 data: $r_S = 0.58$, $N = 24$, $p < 0.01$). Thus there was a tendency for larger setts to have more used entrances, but the number of used entrances did not grow in direct proportion to sett size.

There was no significant correlation between main sett size in 1970 and 1990 (Spearman test, $r_s = 0.24$, $N = 24$, $p = 0.26$), indicating that the rate of growth of main setts was not proportional to their original size. Nor was the percentage change in number of entrances related to the presence or absence of cover (Mann-Whitney test, $W = 113$, $N1 = 7$, $N2 = 11$, $p = 0.47$), indicating that open and covered setts grew in size at about the same rate. However, there was a just significant correlation between number of used entrances in 1970 and in 1990 (Spearman test, $r_s = 0.40$, $N = 24$, $p = 0.05$), suggesting that main setts that were relatively extensively occupied in 1970 continued to be so two decades later.

Table 1. Number ot setts with a given status in each of the two surveys. M denotes main sett, O denotes outlier, – denotes that the sett was absent at the time of the survey.

Status in 1970	Status in 1990	Number of setts	Description
M	M	24	Persisted as main sett
O	O	11	Persisted as outlier
M	O	1	Main sett → outlier
O	M	14	Outlier → main sett
–	M	32	New main sett
–	O	131	New outlier
M	–	5	Main sett which disappeared
O	–	10	Outlier which disappeared

Table 2. Number of entrances (mean and s. d.) at main setts in each of the two surveys.

Measure	Mean		Significance
	1970	1990	
Total entrances	15.9 (8.1)	26.5 (12.7)	$p < 0.01$
Used entrances	5.4 (2.6)	6.0 (3.7)	$p = 0.62$
% used entrances	38.0 (16.0)	24.9 (15.8)	$p = 0.01$

The 11 outliers that persisted from 1970 to 1990 did not change significantly in size (Wilcoxon test, $Z = -0.97$, $N = 11$, $p = 0.33$) or in number of used entrances ($Z = -1.19$, $N = 1$, $p = 0.23$).

Setts persisting from 1970 to 1990 but changing in status

Only one sett changed status from main sett to outlier and no habitat change was involved: the site remained without cover during the 20-year period. The 14 outliers that changed into main setts (Tab. 1) showed no significant difference in size or usage in 1970 when compared with 11 outliers which persisted over the 20-year period without changing status (total number of entrances: Mann-Whitney test, $W = 201$, $N1 = 11$, $N2 = 14$, $p = 0.31$; number of used entrances: $W = 207$, $N1 = 11$, $N2 = 14$, $p = 0.17$). That is, outliers which became main setts by 1990 were originally no larger or smaller than those which remained outliers. No habitat change was evident in any of the 14 cases: 10 setts remained in cover while 4 remained without cover. Outliers that changed status were no more or less likely to be in cover, or in the open, than outliers that persisted (χ_2=0.76, $df = 1$, $p = 0.38$).

New setts

Thirty two main setts and 131 outliers arose de novo since the 1970 survey (Tab. 1). The new main setts were significantly smaller in 1990 than main setts which persisted from 1970 (Mann-Whitney test, $W = 742$, $N1 = 24$, $N2 = 32$, $p < 0.01$) but they did not have a significantly different number of used entrances (Mann-Whitney test, $W = 870$, $N1 = 24$, $N2 = 32$, $p = 0.49$).

Of the 32 new main setts, 17 were in cover and 15 on open downland; of the 131 new outliers, 63 were in cover and 68 in the open.

Setts which disappeared

Five of the main setts that were identified in 1970 could not be found in the 1990 survey (Tab. 1). There was no significant difference in size or usage in 1970 between the five setts that subsequently disappeared and the other 24 main setts that persisted (Mann-Whitney test; total entrances: W = 79.5, N1 = 5, N2 = 24, p = 0.82; used entrances: W = 76.5, N1 = 5,

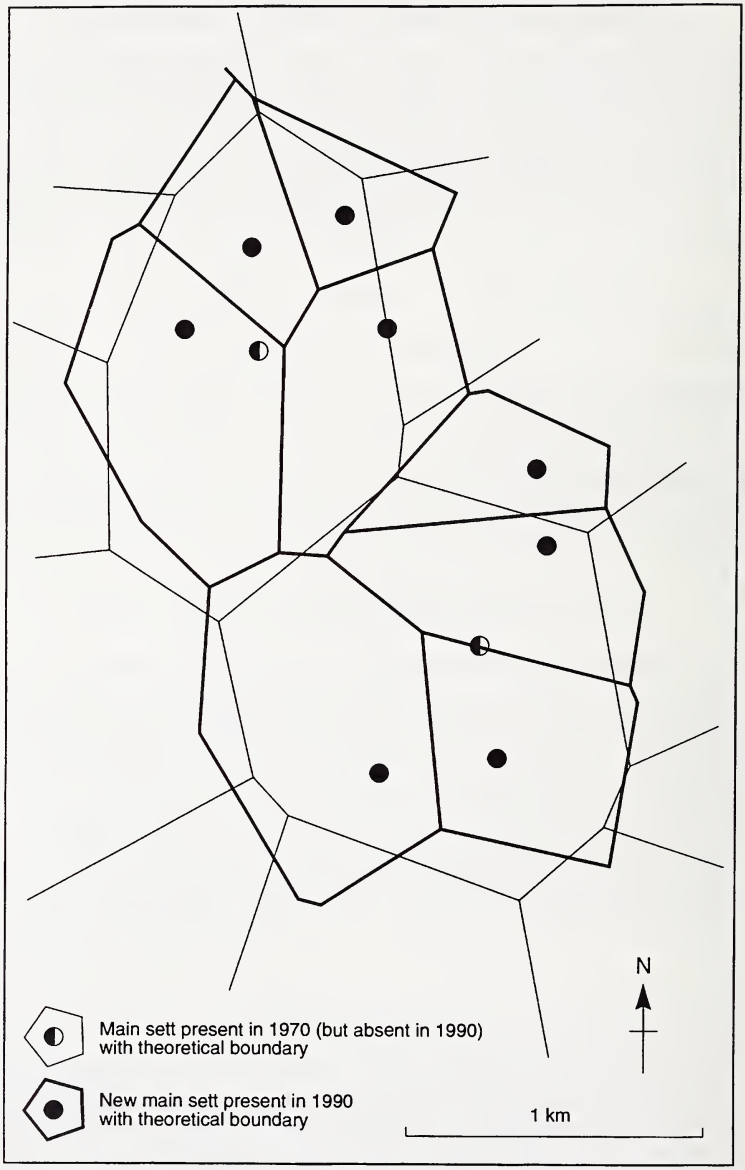

Fig. 1 a

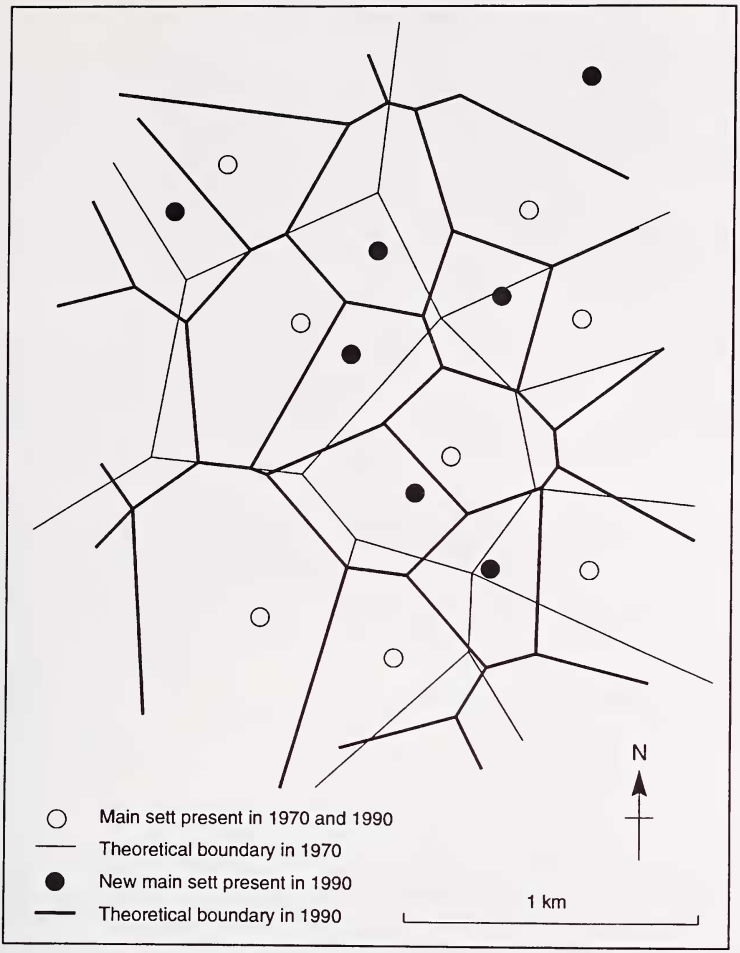

Fig. 1. Main sett locations and corresponding territory boundaries, estimated using Dirichlet tessellation. Thin lines: territory boundaries in 1970; thick lines: territory boundaries in 1990. (a) Cases in which main setts disappeared and the corresponding large territories were subdivided. Half-filled circles: main setts present in 1970 but absent in 1990; filled circles: main setts absent in 1970 but present in 1990. (b) Cases in which main setts persisted but new setts were established nearby, causing the original territories to shrink in size. Open circles: main setts present in both 1970 and 1990; filled circles: main setts absent in 1970 but present in 1990.

N2 = 24, p = 0.95). In four of the five cases, disappearance of the sett was attributable to habitat change (conversion of permanent pasture or scrub to arable). In the remaining case, the main sett was in a small wood close to a housing estate. It is probable that disturbance by humans caused this sett to be abandoned since the 1990 survey revealed a new main sett in a less accessible part of the same wood.

The 10 outliers which disappeared (Tab. 1) were not significantly different in terms of size or usage in 1970 when compared with outliers that persisted to 1990 (Mann-Whitney test; total entrances: W = 110.5, N1 = 10, N2 = 11, p = 1.00; used entrances: W = 129.5, N1 = 10, N2 = 11, p = 0.17). In only one of these cases, where open grassland had been converted to arable, was a habitat change implicated.

Changes in territories

When territories were visualised as Dirichlet tesselations, two types of change in territory conformation were evident as a consequence of the appearance of new main setts. In some cases, a main sett commanding a large territory in 1970 had disappeared by 1990 and the original large territory had become divided into several smaller territories, each occupied by a new main sett. Figure 1 a shows two examples of this process, in which two large territories lost their original main setts and apparently became divided into three or four smaller territories. In other cases the original main sett survived but new main setts were established nearby, causing the original large territory to be compressed by the appearance of new adjacent territories. Where this type of change occurred, it resulted in radical restructuring of the pattern of territorial boundaries (Fig. 1 b).

Combining data from both surveys, the number of outliers per territory varied from 0 to 9, with a mode of zero (Tab. 3). Over the range 0 to 4 outliers per territory, this was not significantly different from what would be expected by a random (Poisson) distribution ($\chi^2 = 4.04$, df = 3, p = 0.25). With 5, 6 or 7 outliers per territory, sample sizes were too small to test for a difference between the actual and expected distributions.

Table 3. Frequency distribution of number of outliers per territory, and number that would be expected by a Poisson distribution.

	0	1	2	3	4	5	6	7
Observed	39	26	12	11	4	0	1	1
Expected	45	31	13	4	1	0	0	0

Discussion

Several previous sett surveys have been undertaken in the UK (NEAL 1972; CLEMENTS 1974; CLEMENTS et al. 1988; THORNTON 1988; CRESSWELL et al. 1990; FEORE et al. 1993; SMAL 1993) including one in which a restricted area was resurveyed after a 20-year interval (SKINNER et al. 1991 a, b). The aim of these surveys has been to provide estimates of badger population density in different parts of the UK at different times and to determine the geological and physiogeographical factors affecting sett distribution. The purpose of the present study, by contrast, was to provide detailed information about the fate of individual setts and territories over a 20-year period, within a relatively restricted but comprehensively surveyed area. During the 20-year period the number of main setts more than doubled, with a consequent reduction in average territory size from 0.7 km^2 to 0.3 km^2. Assuming an average of 5.9 adults per social group (CRESSWELL et al. 1990), this suggests that the population density of badgers increased from 7.97 adults/km^2 to 19.0 adults/km^2.

In assessing these results, it is important to ask to what extent the two surveys were comparable. Although care was taken to use the same methods in the second survey as in the first, the second took more time overall and was conducted in winter, when vegetation is less likely to have obscured sett entrances. The first survey may therefore have underestimated the number of outliers, since these are easily overlooked, especially when they have only one or two entrances. However, it is unlikely that either survey failed to detect main setts, which are usually easy to see in the open landscape of the chalk downland. In addition, the fact that "new" main setts (that is, main setts recorded in the second survey but not in the first) had significantly fewer entrances than "old" ones (that is, main

setts recorded in both surveys) is consistent with the assumption that they came into existence relatively recently. In addition, the fact that data from both surveys yielded a similar relationship between total number of entrances and number of used entrances suggests that the two surveys were using similar criteria to measure these variables. Finally, our results are consistent with the large increases in badger population size that have been recorded during the last two decades in other parts of the UK, using capture-recapture data (da Silva et al. 1993; Neal and Cheeseman 1996).

Five main setts (17% of those present in 1970) were lost between the two surveys. Four of these setts were ploughed up and one was probably subject to human interference from a nearby housing estate. This is consistent with the view that main setts are rarely abandoned except in circumstances of extreme disturbance (e. g., Neal 1977; Neal and Roper 1991). Main setts that persisted grew in size, though they did so at the surprisingly slow rate of about one new entrance every two years. This rate did not differ according to the initial size of the sett or to the presence or absence of cover, so it may be consistent enough to provide a rough means of estimating the age of a sett. However, the rate at which new entrances are dug is likely to vary with soil type and to be higher in new setts than in well established ones (Neal pers. comm.).

The fate of outliers was less predictable than that of main setts: of 35 outliers recorded in 1970, only 11 persisted while 10 disappeared and 14 became main setts. Thus main setts do sometimes arise by enlargement of existing outliers but they are more often dug de novo. The outliers that became main setts were no different in size from outliers that persisted or disappeared, nor were they more or less likely to be in cover, so the reason for their choice as future main setts remains obscure: one possibility is that they were located in more easily dug soil.

The modal number of outliers per territory was zero and the mean was only 1.97, which is slightly less than the mean for the UK as a whole of 2.8 outliers per main sett (Cresswell et al. 1989). There was no correlation between the size of a main sett and the number of outliers in the corresponding territory, suggesting that outliers are not a substitute for an inadequately sized main sett (Neal and Roper 1991). Outliers are sometimes used as temporary nocturnal resting places (Kruuk 1989), as daytime sleeping places in the summer (Roper and Christian 1992), as temporary accommodation for dispersing individuals (Christian 1994), as emergency refuges when an animal is threatened (Butler and Roper 1994), or occasionally for breeding (Neal and Cheeseman 1996). However, the existence of outliers is evidently not essential to the continued survival of a social group, since 40% of territories in our study area were found to lack them.

When territory boundaries were estimated using the method of Dirichlet tesselation (Doncaster and Woodroffe 1993) they suggested two patterns of realignment of boundaries consequent upon the appearance of new main setts. In some cases, the territory around an existing main sett became compressed as new main setts and their associated territories were established in the vicinity. In other cases, a main sett which had commanded a large territory disappeared, and the original large territory became subdivided into smaller territories, each with a new main sett. Cases of the latter type indicate that destruction of a main sett, for example by agricultural activities, can result in the fragmentation of social groups and the establishment of new territories.

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Zusammenfassung

Veränderungen in der Größe, dem Status und der Verteilung von Dachsbauen (Meles meles L.) über einen Zeitraum von 20 Jahren.

Die Resultate aus zwei Bestandsaufnahmen (1970 und 1990) zur Größe, zum Status (Hauptbau, Nebenbau) und zur Verteilung von Dachsbauen in einem 22 km^2 großen Gebiet in Südengland wurden verglichen. Den Zeitraum zwischen den Bestandsaufnahmen haben 24 Hauptbaue und 11 Nebenbaue ohne Statuswechsel überdauert, 1 Hauptbau wurde Nebenbau, und 14 Nebenbaue wurden zu Hauptbauen, 32 Hauptbaue und 131 Nebenbaue sind neu enstanden, und 5 Hauptbaue und 10 Nebenbaue sind verschwunden. Hauptbaue, die überdauert haben, sind im Durchschnitt um 1 Eingang pro 2 Jahre gewachsen. Veränderungen im Status eines Baues hingen nicht mit seiner ursprünglichen Größe zusammen oder mit Charakteristika des umgebenden Habitats, aber Habitatsveränderungen oder Störungen durch Menschen schienen in allen Fällen, in denen Hauptbaue verschwanden, eine Rolle gespielt zu haben.

Die Gesamtzahl an Hauptbauen stieg zwischen 1970 und 1990 von 30 auf 70 Hauptbaue, die durchschnittliche Territoriumsgröße fiel von 0,7 km^2 auf 0,3 km^2, die Anzahl Nebenbaue pro Territorium stieg von 1,2 auf 2,0. Wenn eine Dachspopulation wächst, scheinen diesen Ergebnissen zufolge neue Hauptbaue manchmal aus alten Nebenbauen zu entstehen, am häufigsten werden sie gänzlich neu angelegt. Manchmal wird ein Hauptbau in einem großen Territorium von mehreren neuen Hauptbauen abgelöst und das Territorium aufgeteilt; in anderen Fällen überdauert der alte Hauptbau und das zugehörige Territorium schrumpft zusammen, während sich in der Nachbarschaft neue Territorien bilden.

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